

6

Nutritional Ecology of Lichen/Moss Arthropods

JAMES D. LAWREY

- 6.1 Introduction
- 6.2 Lichen Herbivores
 - 6.2.1 Insect Consumers of Lichens
 - 6.2.2 Mite Consumers of Lichens
 - 6.2.3 Other Arthropods That Consume Lichens
 - 6.2.4 Important Nonarthropod Lichen Feeders
- 6.3 Moss Herbivores
 - 6.3.1 Insect Consumers of Mosses
 - 6.3.2 Mite Consumers of Mosses
- 6.4 Feeding Specificity
 - 6.4.1 Mite Preferences
 - 6.4.2 Insect Preferences
 - 6.4.3 Preferences of Other Invertebrate Lichen/Moss Herbivores
- 6.5 Suitability of Lichens and Mosses as Food
 - 6.5.1 Suitability of Lichens
 - 6.5.2 Suitability of Mosses
- 6.6 Directions for Future Research
- References

6.1 INTRODUCTION

Lichens and mosses are apparently not the food of choice of most arthropod herbivores. The reasons for this are not entirely clear as yet, primarily because there are so few workers in the field and, as a consequence, so few

data. This is unfortunate, because arthropod consumption of lichens and mosses is, by its relative infrequency in nature, worthy of study. Especially needed are investigations into the nutritional ecology of those few herbivores that successfully use lichens and mosses as food. How do these herbivores differ, biologically and ecologically, from others? What factors influence their food choices? How do differences in the nutritional quality of lichens and mosses influence these choices? Some of these questions are addressed in this chapter.

One may question the inclusion of both lichen and moss herbivores in this discussion. Lichens and mosses are phylogenetically unrelated groups that differ in numerous chemical, structural, and physiological characteristics. For example, mosses are green plants fully capable of photosynthesis, whereas lichens are fungi that must obtain their food from colonies of captured algae maintained in the lichen body (called a "thallus"). The lichen thallus is therefore a dual structure, and a herbivore may feed on the entire thallus or specialize on either algal or fungal portions of the thallus.

Despite these and other differences between lichens and mosses, however, there are numerous ecological similarities. That these plants tend to be relatively small, long-lived, and perennial means they are exposed to ecologically similar groups of herbivores. It is for this reason that herbivores of both lichens and mosses are discussed together in this chapter.

A brief survey of the various arthropod consumers of lichens and mosses is provided as an introduction to the range of associations currently known; however, this should not be considered a comprehensive treatment. Economy requires that emphasis be placed on a discussion of those factors that influence the nutritional ecology of the herbivores. Much of the rather extensive and interesting literature dealing with all manner of arthropod associations with lichens and mosses, including concealment, camouflage, dispersal and so forth, must therefore be left out. There are, however, a number of excellent recent reviews available (Gerson, 1969, 1973; Harding and Stuttard, 1974; Gerson and Seaward, 1977; Seyd and Seaward, 1984). In addition, the early, primarily nineteenth century literature on lichen consumption by arthropods was reviewed by Smith (1921).

6.2 LICHEN HERBIVORES

Representatives of numerous terrestrial and aquatic invertebrate groups are known to consume lichens. The terrestrial fauna has been studied most extensively by far. This includes mainly insects, mites, and gastropods. The aquatic fauna includes protozoans, nematodes, oligochaetes, tardigrades, and rotifers, all of which are active only when lichens are wet.

This section briefly reviews what we currently know about arthropod consumers of lichens. Because these arthropods are mainly part of the terrestrial fauna, little mention will be made of the aquatic groups, which are

discussed by Gerson and Seaward (1977). There is also a short section on important nonarthropod lichen invertebrates, mainly gastropods.

6.2.1 Insect Consumers of Lichens

Of the wingless insects (Apterygota), a number of collembolans (springtails) and thysanurans (bristletails) have been reported to feed on lichens, although the details of the interactions are very poorly known. Benedetti (1973) found that the thysanuran *Neomachilis halophila* consumed algal cells from an unidentified crustose (a lichen growth form in which the thallus is closely appressed to the substrate) lichen on intertidal rocks in California. A variety of other food items, including yeast and pine pollen, were also consumed. Other machilids are apparently also associated with lichens (Colman, 1939; Kühnelt, 1976), although little information about their feeding behavior is available. Individuals of the machilid *Machiloides banksi*, which I have observed on a number of occasions in oak woodlands in Maryland, consume lichens along with a variety of other food items (unpublished observations).

A number of springtails have been found to consume lichens. Hale (1972) described a particularly heavy infestation of *Hypogastrura packardii* that led to the destruction of numerous thalli of *Pseudoparmelia baltimorensis* in Maryland. Between August and November of 1970, Hale observed a progressive removal of the upper fungal layers and the algal layer of many thalli. This damage was recorded photographically (Fig. 6.1). Hale estimated that at least 50% of the lichen colony had been lost by the end of the season. A thorough inspection of the habitat revealed thousands of springtails under the turf mat surrounding the lichen-covered rocks. Specimens of *H. packardii* were captured and reared in the laboratory with lichens provided as the only food.

Other investigators have also observed collembolan infestations of lichens (Seaward, 1975; Gerson and Seaward, 1977). Whether these events are so rare they are unimportant to either the lichens or the collembolan populations remains to be determined. However, lichens are apparently an important food source for many species of springtails, and the nutritional ecology of these animals, particularly during periods of unusually high densities, deserves further investigation.

Of the winged or secondarily wingless insects (Pterygota), the Psocoptera and Lepidoptera include the most known lichen herbivores, although many other orders have representatives that feed on lichens. One of the most thoroughly studied of insect herbivore groups is the Psocoptera (psocids or bark lice). Like the collembolans, psocids are known to do extensive damage to lichen colonies (Broadhead and Thornton, 1955; Broadhead, 1958; Seaward, 1965; Laundon, 1971; Richardson, 1975). Seaward (1965) described the feeding habits of *Cerobasis guestfalicus*, a parthenogenetic psocid species from Lincolnshire, U.K., that apparently consumes the orange lichen

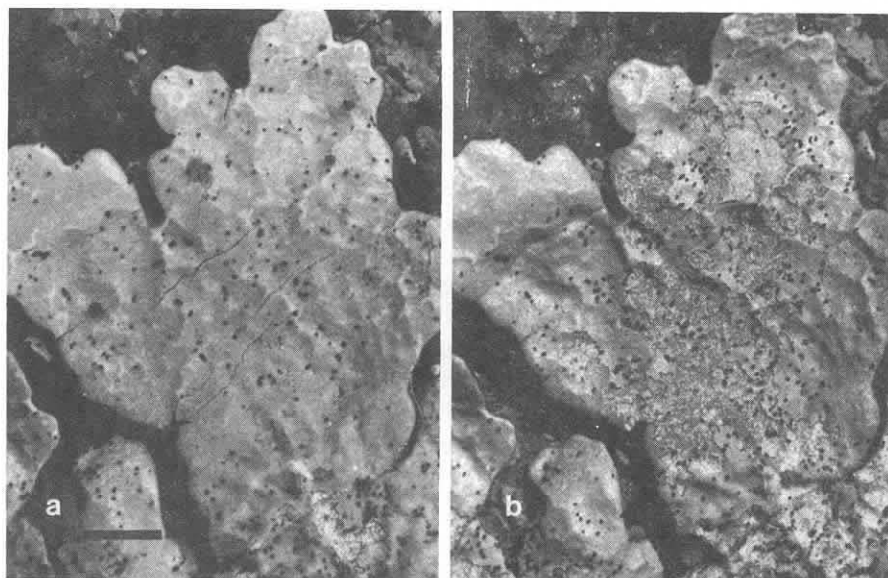


Fig. 6.1 Single lobe of *Pseudoparmelia baltimorensis* photographed on Plummers Island, Maryland, at different times showing different stages of infestation by *Hypogastrura packardii*. Scale = 1 mm. (a) September 13, 1970; (b) October 4, 1970. Reprinted with permission from Hale, M. E. 1972. *Proceedings of the Biological Society of Washington*, Volume 85, pages 287–296.

Xanthoria parietina. An examination of the gut contents of collected individuals revealed mostly *X. parietina* fragments. Laundon (1971) observed lichen communities from two areas in Northumberland, U.K., that had been destroyed by the psocid *Reuterella helvimacula*. The damage appeared to be localized but very heavy. The outer fungal tissues and algal layer of the dominant lichens, *Evernia prunastri* and *Hypogymnia physodes*, had been eaten away, exposing the underlying white fungal tissues.

Not all psocid species are lichenophilous, however. Broadhead (1958) discovered a psocid community on larch trees in Britain dominated by nine species, only two of which feed on lichens. The two species were observed to actively consume the crustose lichen *Lecanora conizaeoides*, and they also grazed the alga *Desmococcus* sp. and fungal spores when the lichen was unavailable. The other seven species consistently ate *Desmococcus* and rarely consumed the lichen (see also Section 6.4.2).

Larvae of a number of butterflies and moths (Lepidoptera) have been reported to consume lichens. Richardson (1975) listed moths from a number of different families known to eat lichens, to camouflage themselves as lichens, or both. Of these, the Psychidae (bagworms) contain a large number of lichen feeders. McDonogh (1939) made a particularly detailed study of the

psychid moth *Luffia ferchaultella* from southern England that apparently feeds almost exclusively on a lichen species identified as *Lecanora varia*. The moth is parthenogenetic and wingless, and the larvae are case bearers. They occur most commonly on trees but occasionally on rocks if the lichen is present. The larvae sometimes eat algae (*Desmococcus* sp.) but apparently prefer lichens, inasmuch as their numbers on rocks and trees are positively correlated with the area covered by *L. varia*.

Other moth families with lichen feeders include the Arctiidae, Crambidae, Ctenuchidae, Gelechiidae, Geometridae, Noctuidae, Nolidae, and Tineidae. Lichen feeding is not characteristic of any of these families but is rather an unusual habit of individual species or occasionally small groups of species within each family.

Sigal (1984) recently discovered near Oak Ridge, Tennessee, an interesting association between a noctuid moth *Zanclognatha theralis*, and the lichen, *Usnea strigosa*. The small (about 2 cm long) larvae are gray-green and look remarkably like the lichen on which they feed, bearing small light-colored patches that mimic the papillae of the lichen (Fig. 6.2a). The adults have light tan wings with fringed margins and black markings (Fig. 6.2b) that appear to camouflage them against a lichen background, although not as well as the larvae. As Sigal mentioned, some moths are known to consume lichens as larvae and to mimic lichens as adults, but rarely have lichen-feeding moths been observed to mimic their host as closely as *Z. theralis*.

Some beetles (Coleoptera) are known to consume lichens. Two lichen-feeding tenebrionids were described by Wessels and colleagues (1979) from the Namib Desert of Southwest Africa. These species were observed feeding on thalli of the lichen *Teloschistes capensis*; although little is known about

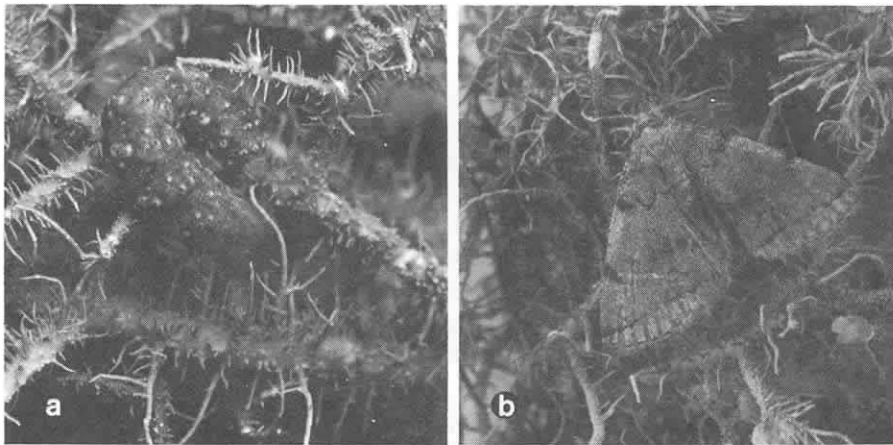


Fig. 6.2 *Zanclognatha theralis* on the lichen *Usnea strigosa*. (a) Larva; (b) adult. Reprinted with permission from Sigal, L. L. 1984. *Bryologist* 87, 66–68. Copyright 1984 of *The Bryologist*.

their nutritional ecology, they are apparently opportunistic feeders that are not restricted to lichens. Other lichen-feeding beetles are apparently more specialized. Holloway (1970) described two species in a new genus of flightless beetles from New Zealand in the Anthribidae that consume lichens. One species, *Lichenobius silvicola*, lives in holes tunneled in the outer bark of various tree branches covered with lichens and algae, and the other, *L. littoralis*, excavates similar tunnels in rock-inhabiting lichens from spray-zone habitats. Nothing is known about the nutritional ecology of either of these species.

Other insect groups are far less frequently associated with lichens. Dipterans (Empididae and Cecidomyiidae) were observed on *Parmelia* lichens by Stebaev (1963), and Richardson (1975) reported that larvae of another dipteran in the Lycorridae (= Sciaridae) feed on lichens. Kalshoven (1958) remarked that termites in the genus *Hospitalitermes* feed exclusively on lichens (unnamed). Some stoneflies (Coleman and Hynes, 1970), earwigs (Smith, 1921), and web spinners (Ross, 1966) have also been reported to feed on lichens. Practically nothing is known about any of these associations.

6.2.2 Mite Consumers of Lichens

Mites (Acari) from numerous groups have been observed to feed on lichens. By far, however, the largest category of lichen feeders is the Oribatei (the moss or beetle mites). These are discussed along with other lichen—oribatid associations in a recent review by Seyd and Seaward (1984). Numerous oribatid species have been reared or cultured in the laboratory with lichens as food (Michael, 1883–1887; Grandjean, 1950; Woodring and Cook, 1962). Others have been found grazing on or burrowing within lichen thalli in the field. The extent to which lichen feeding by these oribatids represents a specific preference is not known in most cases. Travé (1963, 1969) reported that some oribatids are exclusively lichenophilous, whereas others are opportunistic generalists.

Prostigmatid mites (Actinedida) are observed feeding on lichens far less frequently than oribatids. Nevertheless, there are some interesting accounts of lichen feeding by these mites. The family Tydeidae apparently includes a number of lichen feeders. In Antarctica, *Tydeus tilbrooki* is known to feed on lichens (Gressitt and Shoup, 1967; Strong, 1967). Gerson (1968) reported that another tydeid, *Paralorryia mali*, consumes lichens. Also, a study of microarthropods associated with bark-inhabiting fruticose (a shrubby or hairlike growth form) lichens in Belgium (Andre, 1979) revealed that the prostigmatid mites outnumbered all other mite groups, with the Tydeidae the most dominant family.

The prostigmatid gall mites (Eriophyoidea) include a few species that form galls on lichens (Mani, 1964), although little is known about them or the gall-forming process in parasitized lichens. A few astigmatid mites (Acari-dida) have been found in association with lichens (Hughes and Tilbrook,

1966; Andre, 1975, 1979; Fain, 1975), but the degree to which lichens are consumed by these mites is not known. Mesostigmatid mites (Gamasida) are sometimes observed in association with lichens (Evans et al., 1961; Stebaev, 1963; Travé, 1963; Tilbrook, 1967; Andre, 1975, 1979). Because many of these are predacious, however, they are probably not as important as other groups insofar as lichen herbivory is concerned.

6.2.3 Other Arthropods That Consume Lichens

A few other arthropod groups include lichen feeders. Zopf (1907) reported the occurrence of a diplopod (*Polyxenus*) in galls formed on thalli of the lichen *Ramalina kullensis* in Sweden. Nothing further is known of this association. Colman (1939) observed an isopod, *Campecopea hirsuta*, and an amphipod, *Hyale nilssoni*, in stands of the intertidal zone lichen *Lichina pygmaea*. The isopod feeds only when the lichen is wet. Wieser (1963) also studied the feeding ecology of *C. hirsuta* and found that it apparently consumes the algal symbiont of *L. pygmaea* and leaves the fungal partner almost completely untouched. Other strictly terrestrial isopods of the Oniscoidea are reported to be fairly abundant in lichens sampled from Belgium (Andre, 1979).

6.2.4 Important Nonarthropod Lichen Feeders

Brief mention must be made of the mollusks (Gastropoda and Bivalvia), an important nonarthropod group that includes some lichen feeders. Terrestrial snails and slugs have long been observed to consume lichens (Smith, 1921; Plitt, 1934; Coker, 1967; Peake and James, 1967; Yom-Tov and Galun, 1971; Lawrey, 1980, 1983). Digestive enzymes capable of breaking down the common lichen polysaccharide, lichenin, have been found in snail and slug guts (Holden and Tracey, 1950; Nielsen, 1963) along with a diverse array of other polysaccharidases (Runham and Hunter, 1970; Runham, 1975). Lichen consumption by snails and slugs is probably opportunistic and nonspecific for the most part, but few generalizations can be made, because so little is known about the feeding ecology of these species. Snails and slugs have sometimes been used by investigators in laboratory tests to determine whether various lichen phenolic compounds afford lichens protection from grazers (Zukal, 1895; Stahl, 1904; James and Henssen, 1976; Lawrey, 1980, 1983; Section 6.5.1).

In intertidal marine environments, several species of periwinkles (*Littorina*) are found in zones dominated by lichen species in the genus *Verrucaria* (Colman, 1939; Stephenson and Stephenson, 1972). Limpets (*Patella* spp.; Fletcher, 1973) and bivalves, especially *Lasaea rubra* (Colman, 1939), are also probably important lichen herbivores in these environments, but little is known about their nutritional ecology.

6.3 MOSS HERBIVORES

Gerson (1969) reviewed moss–arthropod associations, including moss consumption, along with other topics (dispersal, camouflage, etc.). If one is to judge by the information currently available, mosses appear to be consumed by arthropods even less frequently than lichens. There are, however, a few reports, and these will be mentioned briefly. There are two major groups of arthropod consumers of mosses: insects and mites.

6.3.1 Insect Consumers of Mosses

Only occasional reports of moss feeding by insects have appeared in the literature, and no single insect group is dominant. Indeed, numerous insect orders include moss consumers. Collembolans have been observed feeding on mosses in Antarctica (Pryor, 1962; Janetschek, 1967) and have been reared on mosses in the laboratory (Pryor, 1962). Additional evidence comes from McMillan and Healey (1971), who found moss fragments in the gut contents of the collembolan *Tomocerus*.

Other moss feeders include caterpillars of a few species in the primitive lepidopteran suborder Zeugloptera (Chapman, 1894; Tillyard, 1923), several species of crane flies (Tipulidae) (Alexander, 1920), an Australian mecopteran, *Choristes* (Tillyard, 1926), two species of pygmy grasshoppers (Tetrigidae) (Verdcourt, 1947), and tingoid bugs (*Acalypta*; Bailey, 1951). Numerous aphids have also been reported from mosses (Börner, 1952), and ants have been observed feeding on moss capsules (Plitt, 1907).

Aquatic insect larvae have occasionally been reported from species of *Fontinalis*, an aquatic moss genus with representatives in North America, Europe, Asia, and Africa. These include dipterans in the Tipulidae (Alexander, 1920) and Empididae (Brindle, 1964) and mayfly naiads (Jones, 1949).

6.3.2 Mite Consumers of Mosses

Mites representing most suborders are found in damp, shaded habitats containing mosses, but there is only the scantest evidence that mosses are actually eaten by these animals. This is probably because few investigators have looked into the possibility. A number of oribatid mites have been reared on mosses for varying lengths of time under laboratory conditions (Sengbusch, 1954; Woodring, 1963). Moss remains have also been observed in gut contents collected from 4 out of 40 species of oribatids examined by Schuster (1956).

Some prostigmatid mites (Actinedida) are also known to feed on mosses. Gerson (1972) studied eleven species of the prostigmatids (*Ledermuelleria*: Stigmaeidae) collected from various moss habitats in Canada and the northeastern United States. He found that some mites are associated with many mosses but that oviposition occurs on only a few preferred species. The

feeding ecology of one species, *L. frigida*, was studied in the laboratory. These mites apparently pierce stem and leaf tissues with their chelicerae and suck out the contents of some of the cells. Continued feeding results in discoloration and even shriveling of some young shoots. Other muscivorous mite species will undoubtedly be discovered as moss-mite associations continue to be investigated.

6.4 FEEDING SPECIFICITY

The degree of feeding specificity among arthropod consumers of lichens and mosses is probably very low, although generalizations are difficult to make because of the observational or anecdotal nature of the literature on lichen/moss-arthropod associations. For the most part, however, the available evidence suggests that lichen and moss herbivores tend to be generalist feeders that frequently include a variety of other food items in their diets. The reasons why there are so few herbivores specialized on lichens and mosses have not been adequately investigated but probably include the low nutritional quality of most lichens and mosses and the presence of allelochemicals that deter generalist herbivores (Section 6.5).

Given the general lack of specialized feeding on these plants, those few herbivores known to prefer lichens or mosses over other foods are extremely interesting. These animals and their food preferences are considered below. Unfortunately, very little is known about the causes of preferences for lichens and mosses, and even less is known about how discriminatory feeding among lichens and mosses influences an animal's nutritional ecology. These are clearly areas requiring further experimental investigation.

6.4.1 Mite Preferences

Comprehensive community-level studies of oribatids have provided indirect evidence for lichen and/or moss preferences by some species. Travé (1963, 1969) found that some oribatids are associated most frequently with rock-inhabiting lichens and others with bark-inhabiting lichens. Still others apparently have broader preferences, being found in both mosses and lichens. Other studies (Granjean, 1936; Travé, 1961; Andre, 1975, 1979) have shown similar patterns.

These studies are interesting because they indicate a degree of preference under natural conditions that may reflect nutritionally important resource specificity. However, it is difficult to separate habitat preferences from food preferences without experimental evidence or very close observation. For example, Andre (1979) found that a number of mite species appeared to be associated with particular bark-inhabiting fruticose lichens in Belgium. On closer examination of the distributional data, however, he concluded that species were more closely associated with the tree species bearing the li-

chens than with the lichens themselves. This suggests that habitat, not nutritional factors, is responsible for the presumed preference.

Studies of mite communities in littoral zone habitats (Gjelstrup and Søbchting, 1979; Colloff, 1983) have also shown associations between various mite species and lichens inhabiting rocks of varying distances from the shore. As with other habitat preference studies, it is difficult to determine whether these associations are due to preferences for lichens as foods or for various microhabitats. In a littoral zone habitat in Denmark, Gjelstrup and Søbchting (1979) found one mite species, *Phauloppia coineaui*, that apparently is very discriminating in its choice of lichen foods. This species seems to select the fruticose lichen *Ramalina siliquosa* and avoid a close relative, *R. cuspidata*. Its preference for *R. siliquosa* is apparently due to the loose medullary structure of this lichen, which provides a better shelter as well as a food supply.

Mite preferences for lichens or mosses have rarely been investigated experimentally in the laboratory, although this is the only way to demonstrate nutritionally important preferences. Gerson (1972) studied the feeding ecology of the prostigmatid mite, *Ledermuelleria frigida*, specimens of which were collected from various moss species in Canada and the northeastern United States. Preliminary field observations suggested that this mite preferred certain moss species over others, so a number of interesting laboratory studies were designed to explore this more fully. Previously starved female mites were placed on 32 different moss species under identical culture conditions and observed for 15 days. If the mites laid no eggs and walked away after 2–3 days, the experiment was scored “no survival.” If mites consumed the moss but laid no eggs, it was scored “survival but no oviposition,” and if eggs were also laid, it was scored “survival and oviposition.” Results of these experiments (Table 6.1) indicate that female *L. frigida* are able to use a variety of mosses as food but lay eggs on only a few. These preferred species are also those on which *L. frigida* is observed in the field. Failure to survive on some moss species is apparently related more to mechanical factors (thickened outer cell walls or extra layers of tissue covering moss leaves) than to nutritional or chemical factors.

In their study of the Antarctic mite *Alaskozetes antarcticus*, Young and Block (1980) observed definite preference for the lichen *Xanthoria candelaria* when offered a choice between the lichen, a green alga (*Prasiola crispa*), and penguin guano. Experiments were then designed to determine whether different food materials affected metabolism of the animals. Three groups of mites were cultured at 10°C, each provided with one food type. The results indicate that rates of respiration (per individual) and metabolism (per gram body weight) were highest in animals maintained on the lichen, suggesting that the lichen is the most nutritionally suitable food and is rapidly utilized. Thus, these mites apparently choose food on the basis of its nutritional value.

Additional laboratory studies of mite feeding preference are needed to

Table 6.1. Survival and Oviposition of the Mite *Ledermuelleria frigida* on 32 Moss Species under Laboratory Conditions

Survival and oviposition	Survival but no oviposition	No survival
<i>Amblystegium serpens</i>	<i>Bryum argenteum</i>	<i>Atrichum altecristatum</i>
<i>Barbula unguiculata</i>	<i>Bryum pseudotriquetrum</i>	<i>Leucobryum glaucum</i>
<i>Brachythecium salesbrosum</i> ^a	<i>Dicranum scoparium</i>	<i>Pogonatum urnigerum</i>
<i>Brachythecium</i> sp.	<i>Ditrichum pusillum</i>	<i>Polytrichum commune</i>
<i>Ceratodon purpureus</i>	<i>Fissidens taxifolius</i>	<i>Polytrichum piliferum</i>
<i>Didymodon tophaceus</i>	<i>Funaria hygrometrica</i>	
<i>Drepanocladus aduncus</i>	<i>Hedwigia ciliata</i>	
<i>Heterophyllum haldanianum</i> ^a	<i>Mniobryum wahlenbergii</i>	
<i>Hypnum lindbergii</i> ^a	<i>Mnium cuspidatum</i>	
<i>Hypnum reptile</i> ^a	<i>Mnium rugicum</i>	
<i>Leptodictyum riparium</i> ^a	<i>Pleurozium schreberi</i>	
<i>Thuidium delicatulum</i>	<i>Racomitrium heterostichum</i>	
	<i>Rhodobryum roseum</i>	
	<i>Sphagnum magellanicum</i>	
	<i>Sphagnum recurvum</i>	

Source: Gerson (1972); reprinted with permission from *Acarologia*.

^a *L. frigida* present in field collections.

better understand apparent preferences for lichens and mosses in the field. These studies should be designed to determine not only what species of lichens and mosses are consumed but also the nutritional quality of those species that are consumed. This is an area about which we know very little. As Woodring (1963) has mentioned, mites may readily consume a low-quality food, but it may take several generations for dietary deficiencies to become apparent. Also, different developmental stages (larvae, nymphs, adults) may require different quality resources. For example, it is known that immatures of *Mycobates parmeliae* are frequently associated with lichens; however, adults are found most frequently in mosses and hepatics (Travé, 1963). Whether this is due to nutritional or other factors is not known.

6.4.2 Insect Preferences

A survey of the lichen/moss herbivore literature reveals fewer examples of food preferences among the various known insect herbivores than for mites. This is probably the result of differences in the approaches usually taken to

study the two groups. Entire species assemblages of mites can be extracted from lichen and moss material, thereby providing a large amount of species-substrate association data that can be used to infer possible food preferences. Insects, however, are usually studied as isolated individuals or groups of conspecifics, and the full range of feeding preferences is much more difficult to estimate under field conditions. Unfortunately, few laboratory studies of insect feeding on mosses and/or lichens have been done, so it is difficult to make generalizations.

A few field observations suggest a certain degree of feeding specificity by insect consumers of mosses and lichens. The collembolan *Hypogastrura packardii* was found to consume only the upper fungal portion and algal layer of the rock lichen *Pseudoparmelia baltimorensis*, leaving untouched the white medullary layer below the algal cells (Hale, 1972). Hale suggested that this feeding behavior resulted from an avoidance of phenolic compounds, notably protocetraric acid, produced in the medullary tissues of the lichen. It may also reflect a preference for algae, but this was not determined experimentally.

Sigal (1984) observed numerous larvae of the moth *Zanclognatha theralis* in field collections of the lichen *Usnea strigosa* from Tennessee. These animals apparently restrict their diet to this lichen, because no other food items were ever taken, and larvae completed their development under laboratory conditions with only *U. strigosa* material as food. Because larvae of *Z. theralis* look remarkably like the lichen (Fig. 6.2), a high degree of host specificity would be expected. A more complete study of the nutritional ecology of this insect species would certainly be of interest.

By far the best-documented case of food preferences by insect lichen feeders is that of Broadhead (1958), who studied nine psocid species found on larch trees in northern England. Of these, seven species clearly prefer a terrestrial alga, *Desmococcus* sp., and two species apparently prefer the lichen *Lecanora conizaeoides*. These preferences were initially inferred from field observations and confirmed by laboratory tests; both nymphs and female adults were consistently found on the preferred resource (Table 6.2).

The lichen grazers differ in their preference for different portions of the lichen. *Reuterella helvimacula* eats all portions of the thallus, whereas *Elipsocus mclachlani* feeds only on fruiting structures. This was initially interpreted as an avoidance of medullary substances produced by the lichen, but this interpretation has since been discounted (Gerson and Seaward, 1977). Laboratory tests revealed that the lichen consumers are able to switch to the alga in the absence of the lichen; however, the alga consumers starve before eating the lichen. Also, the lichen consumer, *Elipsocus mclachlani*, seems able to assimilate the alga better than the lichen, inasmuch as its oviposition rate is higher when fed the alga than when fed the lichen. For the other lichen consumer, *Reuterella helvimacula*, oviposition rates are the same when fed either the lichen or alga. These results suggest that the alga may generally be a better food than the lichen and that only one psocid species in

Table 6.2. Occurrence of Nymphs and Adult Females of Nine Psocid Species on Experimental Larch Twigs Half Covered with the Alga *Desmococcus* sp. and Half Covered with the Lichen *Lecanora conizaeoides*

Species of psocids	Number of nymphs		Number of adult females	
	Alga	Lichen	Alga	Lichen
Species preferring alga				
<i>Mesoposocus immunis</i>	14	4	28	10
<i>M. unipunctatus</i>	17	0	22	10
<i>Amphigerontia bifasciata</i>	34	2	22	0
<i>A. contaminata</i>	30	4	21	6
<i>Philotarsus picicornis</i>	36	2	36	3
<i>Elipsocus westwoodi</i>	62	22	35	1
<i>E. hyalinus</i>	29	8	32	6
Species preferring lichen				
<i>E. mclachlani</i>	9	28	16	27
<i>Reuterella helvimacula</i>	23	84	4	28

Source: Reprinted with permission from Broadhead, E. 1958. *J. Anim. Ecol.* **27**, 217–263. Copyright 1958 Blackwell Scientific Publications, Ltd.

this assemblage, *R. helvimacula*, is completely adapted to a lichen diet. The other lichen consumer, *E. mclachlani*, is apparently only partially adapted to such a diet, although it consistently chooses the lichen over the alga when both are available in adequate amounts.

6.4.3 Preferences of Other Invertebrate Lichen/Moss Herbivores

Examples of other groups of lichen and moss consumers that exhibit food preferences of ecological importance are rare in the literature. One example is provided by Wieser (1963), who observed the feeding behavior of two intertidal isopods in the Sphaeromatidae. One of these, *Campecopea hirsuta*, feeds almost exclusively on the blue-green algal associate of the lichen *Lichina pygmaea*. Whether this represents a preference for the alga or an avoidance of the fungus is not known.

Other examples of lichen/moss herbivore preference involve gastropods. Smith (1921) and Coker (1967) have described a number of studies by various investigators that demonstrate feeding specificity by snail and slug consumers of lichens and mosses. Coker (1967) adds to these a brief description of the feeding preferences of the slug *Lehmannia marginata* at various sites in England and Scotland. It apparently consumes a wide variety of lichens and mosses but prefers the fruiting structures of *Pertusaria pertusa* to the vegetative thallus. Also, it avoids contact with *P. amara*, a species with a

distinctive chemistry that commonly grows along with *P. pertusa*, but the causes of these feeding preferences were not investigated.

In their examination of the feeding habits of two desert snails, Yom-Tov and Galun (1971) discovered that a wide variety of food items, including mosses and lichens, are consumed. It appeared, however, that the snails consistently ate lichens (*Buellia* spp.) that have brown spores and avoided the more abundant *Caloplaca* and *Teloschistes* species, all of which have morphologically distinctive spores. The explanation given for this feeding behavior is the presence of the phenolic compound parietin in the avoided species, although there is no evidence that this substance plays a role in defense against herbivores.

Another slug known to discriminate between various lichen species in both field and laboratory situations is *Pallifera varia* (Lawrey, 1980, 1983), a common species in western Virginia. Field collections on three separate sampling dates showed a high frequency of occurrence of *P. varia* on various crustose lichens, especially *Aspicilia gibbosa* and *A. cinerea*. Laboratory tests demonstrated that lichens are actually being consumed by the slugs. The two preferred lichen species also are among the most dominant in the rock-inhabiting lichen/moss community, suggesting that slugs may be feeding more or less randomly and thus would more likely be found feeding on species they encounter more frequently in the field. To test the hypothesis that slugs are actually feeding preferentially on certain species, the following preference index was used:

$$P_i = \frac{\text{slug utilization frequency of lichen species } i}{\text{percent cover of lichen species } i \text{ in the community}}$$

Results of this analysis revealed a strong preference for *Lasallia papulosa*, *Ochrolechia yasudae*, and the two *Aspicilia* species, and an avoidance of *Pseudoparmelia baltimorensis*; *Xanthoparmelia cumberlandia* was not strongly avoided or preferred (Table 6.3). This suggests that, although slugs feed on a variety of lichen species, some are eaten more frequently and some less frequently than can be accounted for by their relative abundance in the field. This feeding discrimination appears to involve secondary compounds (Section 6.5.1).

6.5 SUITABILITY OF LICHENS AND MOSSES AS FOOD

The relatively low susceptibility of lichens and mosses to arthropod attack is generally explained in two ways: (1) lichens and mosses are low in nutritional value and make poor foods compared with vascular plants; (2) lichens and mosses produce secondary compounds that inhibit invertebrate grazers. Each of these explanations will be considered in the following sections.

Table 6.3. Feeding Preferences of *Pallifera varia* from Field Observations made at Stony Man Mountain Study Area in Virginia^a

Lichen species	Preference
<i>Lasallia papulosa</i> (Ach.) Llano	5.92
<i>Aspicilia gibbosa</i> (Ach.) Körb.	3.78
<i>Ochrolechia yasudae</i> Vain.	3.69
<i>Aspicilia cinerea</i> (L.) Körb.	3.59
<i>Pertusaria</i> sp.	2.06
<i>Xanthoparmelia cumberlandia</i> (Gyel.) Hale	1.13
<i>Pseudoparmelia baltimorensis</i> (Gyel. & For.) Hale	0.17

Source: Reprinted with permission from Lawrey, J. D. 1983. *Am. J. Bot.* **70**, 1188–1194. Copyright 1983 *American Journal of Botany*.

^a The preference index is discussed in the text.

6.5.1 Suitability of Lichens

There is an unusually large literature on lichen nutritional quality owing to the importance of lichens as forage for large vertebrates, most notably the reindeer or caribou (*Rangifer tarandus*; see Richardson, 1975; Richardson and Young, 1977). Inasmuch as the nutritional requirements of vertebrates and invertebrates probably differ to various degrees, a brief survey of this literature will serve only to suggest potential research problems for those interested in arthropod nutrition.

Reviews concerning the nutrient content of ground-dwelling lichens from arctic and subarctic regions (Courtright, 1959; Aleksandrova et al., 1964) suggest a number of patterns. Despite a good deal of variability in nutrient concentrations reported for different species and growing regions, protein content is usually low, along with Ca and P concentrations, and fiber content is generally high (e.g., Table 6.4). In addition to these whole-thallus patterns, there are age-specific differences in lichen nutrient content. Generally, the youngest lichen tissue has the highest nutrient levels.

Defense compound production by lichens probably also influences their susceptibility to herbivores (e.g., Rundel, 1978; Slansky, 1979; Stephenson and Rundel, 1979; Lawrey, 1980, 1983, 1984). Lichens produce numerous secondary compounds, many of which are not found in other organisms. Most are weak phenolic acids of fungal origin that form water-insoluble extracellular deposits on lichen fungal cell walls. Although lichen compounds have very low water solubilities (Iskandar and Syers, 1971), they are apparently soluble enough to be biologically active (Vartia, 1973).

The idea that lichen compounds afford protection against herbivores is not a recent one. Smith (1921) reviewed a considerable body of observations on the subject of lichen chemical defense against invertebrates and vertebrates alike. She and later Coker (1967) summarized the contrasting views of Zukal (1895) and Zopf (1896) on the role of lichen compounds in inhibiting

Table 6.4. Percentage Distribution of Nutrients in Caribou Diet Species Available in the Spring in Newfoundland

Plant species	Protein	Fat	Fiber	Ash	Ca	P
<i>Alnus crispa</i> ^a	30.85	3.35	13.31	4.11	0.42	0.37
<i>Kalmia polifolia</i> ^b	11.43	2.17	16.88	2.75	0.59	0.15
<i>Larix laricina</i> ^a	18.47	5.03	18.59	3.82	0.24	0.27
<i>Scirpus cespitosus</i> ^c	15.87	0.85	27.25	2.85	0.12	0.15
<i>Smilacina trifolia</i> ^c	20.20	2.72	14.52	6.61	0.27	0.48
<i>Cladonia mitis</i> ^d	4.11	2.47	28.22	1.33	0.17	0.05

Source: Reprinted with permission from Bergerud, A. T. 1972. *J. Wildlife Manag.* **36**, 913–923. Copyright 1972 Wildlife Society.

^a Tree leaves.

^b Shrub leaves.

^c Whole herbaceous vascular plants.

^d Whole lichen thalli.

lichen herbivores. Zukal (1895) argued that lichen compounds protect lichens from herbivores. However, Zopf (1896) fed snails potato slices covered with various lichen compounds and found that most elicited little if any avoidance by the herbivores.

Additional studies tend to support Zukal's hypothesis. For example, Stahl (1904) discovered that the snail *Helix hortensis* avoided thalli of some lichens but consumed these same lichens if they had been washed in a weak soda solution to remove lichen acids. Similar results were obtained with wood lice (*Oniscus asper*) and earwigs (*Forficula auricularia*), suggesting that lichen compounds are able to afford lichens a general protection against grazers. However, there have been very few attempts to experimentally test Zukal's defensive compound hypothesis. As a result, inferences have had to be based on indirect evidence. Gerson and Seaward (1977) compiled a list of invertebrate species known to graze lichens and the chemicals produced by the lichen species they were reported to consume. From this listing, it is difficult to discern patterns of ecological significance.

Since Gerson and Seaward's (1977) review, results of a few laboratory experiments have been published demonstrating an herbivore deterrent role for lichen compounds. Slansky (1979) reported results of feeding and growth rate experiments with larvae of the yellow-striped armyworm *Spodoptera ornithogalli*, a polyphagous insect pest. Larvae were offered a choice of broccoli leaves coated with solutions of the lichen compounds atranorin, vulpinic acid, a combination of the two, or no compounds. Results of these preference tests demonstrate that atranorin elicits no significant avoidance by larvae but that vulpinic acid is actively avoided. Larvae were then forced to feed on treated leaves, and their growth rates were compared with those fed untreated leaves. Results of these experiments (Fig. 6.3) suggest that vulpinic acid, despite its inhibition of larval feeding, does not reduce larval

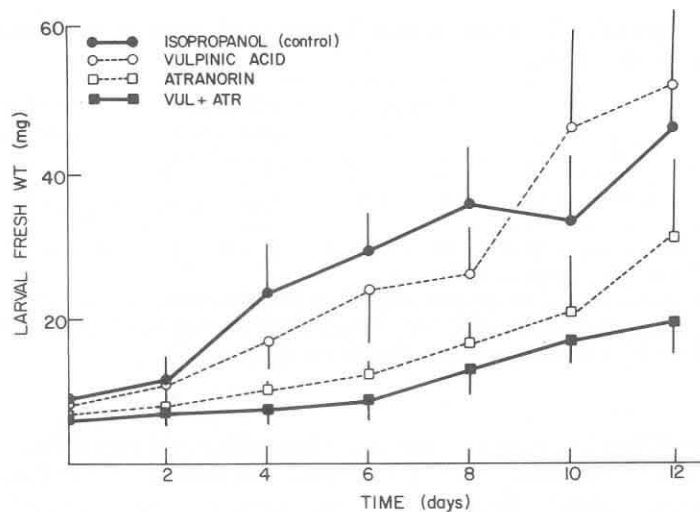


Fig. 6.3 Mean fresh weight (\pm SE) of *Spodoptera ornithogalli* larvae fed broccoli leaves coated with lichen chemicals. From Slansky (1979). Reprinted by permission of the Entomological Society of America.

growth rates. However, atranorin significantly reduces growth of young larvae, and the two compounds together have the greatest inhibitory effect. Slansky concluded from these experiments that vulpinic acid may function as an antiherbivore compound, probably as a repellent, whereas atranorin probably functions as an antibiotic.

Another recent laboratory investigation of the lichen defensive compound hypothesis made use of the slug *Pallifera varia* (Lawrey, 1983). Previous observations (Lawrey, 1980) indicated that this species grazed more frequently on certain lichen species than would be expected if it fed randomly. Two hypotheses were developed to explain this grazing pattern: (1) the *preference hypothesis*, that slugs actively seek out lichens of highest quality; and (2) the *avoidance hypothesis*, that preference by slugs actually results from the rejection of unpalatable species. The preference hypothesis was tested by measuring the concentration of essential elements in lichens eliciting high and low preference by slugs. Lichens with high concentrations of essential elements, especially N and P, were considered to be highest in nutritional quality. If the preference hypothesis is correct, then, preferred species should have the highest concentrations of these elements. In fact, however, preferred lichens (*Aspicilia gibbosa* and *Lasallia papulosa*) have the lowest concentrations of N and P, and avoided lichens (*Pseudoparmelia baltimorensis* and *Xanthoparmelia cumberlandia*) have the highest concentrations of these elements.

The avoidance hypothesis was tested by offering slugs choices of baited filter-paper disks impregnated with extracts of lichens eliciting high and low

Table 6.5. Mean (\pm SE) Percent Area of Experimental Paper Disks Grazed by *Pallifera varia* after 48 hours^a

	<i>Lasallia papulosa</i>	<i>Aspicilia gibbosa</i>	<i>Xanthoparmelia cumberlandia</i>	<i>Pseudoparmelia baltimorensis</i>
Control	18.15 \pm 1.78	30.31 \pm 4.42	31.28 \pm 2.08	17.61 \pm 4.15
Treatment	14.27 \pm 4.38	15.47 \pm 2.74	1.69 \pm 0.39	1.22 \pm 0.78

Source: Reprinted with permission from Lawrey, J. D. 1983. *Am. J. Bot.* **70**, 1188–1194. Copyright 1983 *American Journal of Botany*.

^a Disks were treated with either acetone (control) or a lichen acetone extract (treatment), and after the acetone evaporated, the disks were all baited with a 1% aqueous yeast extract solution and placed in *P. varia* culture chambers. Sample size in all cases is 4.

preference. If this hypothesis is correct, slugs will avoid baited disks treated with extracts of the least preferred lichens. The results (Table 6.5) clearly support this hypothesis. Disks treated with extracts of preferred lichens (*A. gibbosa* and *L. papulosa*) are consumed more heavily than disks treated with extracts of avoided lichens (*P. baltimorensis* and *X. cumberlandia*). These results clearly demonstrate the potential herbivore deterrent role of lichen compounds, and suggest that the lichens of highest nutritional quality to herbivores may present the most effective chemical defense against herbivores. However, further experimental testing is required to assess the generality of this phenomenon.

6.5.2 Suitability of Mosses

Mosses are similar to other green plants in their nutritional composition. They contain the same sugars as higher plants, although some unknown sugars are found in *Sphagnum* mosses (Maass and Craigie, 1964). Lipid concentrations are highest in spores, which may account for observed spore feeding by ants (Plitt, 1907) and female lemmings (Pakarinen and Vitt, 1974). The caloric value of mosses is in the same range as that of higher plants (Bliss, 1962; Forman, 1968; Pakarinen and Vitt, 1974; Rastorfer, 1976). Concentrations of essential elements, especially N, vary extensively from group to group, a situation also seen in higher plants. There is, however, some evidence for generally lower K and Mg levels in mosses than in higher plants (Prins, 1981).

Given these similarities in nutritional quality between mosses and other plants, why are mosses consumed so infrequently by arthropods? The answer likely involves the low digestibility of most mosses and possibly the production of inhibitory compounds. Compared with tree leaves, mosses generally contain lower concentrations of easily digestible soluble carbohydrates and hemicelluloses, and higher concentrations of structural components less easily digested, such as cellulose and polyphenolic ligninlike compounds, although mosses do not produce true lignin (Erickson and Miksche,

Table 6.6. Structural Components of Tree Leaves and Thalli of a Moss (*Polytrichum ohioense*) and a Lichen (*Cladonia cristatella*)

Litter type	Soluble carbohydrates	Hemicellulose	Cellulose	Lignin	Ash
<i>Pinus resinosa</i> leaves	35.41 ^a (1.40)	13.44 (0.70)	19.37 (0.15)	23.56 (0.65)	3.68 (0.29)
Angiosperm tree leaves	43.89 (5.39)	11.59 (1.44)	20.43 (2.15)	11.04 (2.14)	6.97 (0.40)
<i>Polytrichum ohioense</i> thalli	16.51 (0.11)	14.07 (0.07)	24.37 (0.17)	12.90 ^b (0.01)	4.24 (0.16)
<i>Cladonia cristatella</i> thalli	19.93 (1.09)	66.54 ^c (2.01)	2.98 ^c (0.91)	0.78 ^c (0.02)	10.92 (1.36)

Source: Lawrey (1977).

^a All values mean percent (oven dry weight). Values in parentheses are standard errors. Sample sizes are 5 in each case except "angiosperm tree leaves," where N = 9.

^b True lignins are not known from mosses.

^c True hemicelluloses, celluloses, and lignins are not known from lichens. Cell walls are most likely made up of chitin and lichenin.

1974; Miksche and Yasuda, 1978). An example of such a comparison is provided in Table 6.6, in which the structural components of angiosperm tree leaves and leaves of the gymnosperm *Pinus resinosa* are compared with a moss (*Polytrichum ohioense*) and a lichen (*Cladonia cristatella*), using the methods of Goering and Van Soest (1970). The moss has the lowest soluble carbohydrate fraction and relatively high cellulose and "lignin" fractions. Another comparison of the structural components of mosses and both woody and nonwoody plants revealed similar patterns (Skre et al., 1975).

The high concentration of ligninlike polyphenolic compounds is probably of greatest significance. These compounds are known to have an antibiotic action, and several studies have shown the antibiotic activity of compounds extracted from mosses and liverworts (Madsen and Pates, 1952; Pates and Madsen, 1955; Ramaut, 1959; McCleary et al., 1960; Wolters, 1964; McCleary and Walkington, 1966; Gupta and Singh, 1971; Banerjee and Sen, 1979). Presence of these antibiotics is likely to have a negative effect on grazers either directly or indirectly (by inhibiting gut microorganisms), but no studies have been done.

All of these factors probably limit not only arthropod consumption of mosses but also consumption by herbivorous mammals and birds. Prins (1981) recently developed an interesting theory to account for the observation that, at least among vertebrate herbivores, mosses are consumed relatively frequently in arctic and cold-temperate regions and practically not at all in warm climates. Mosses produce a highly unsaturated fatty acid, arachidonic acid, and information available suggests that ingestion of this compound affords protection of cell membranes against very low temperatures. If this is true, moss consumption in cold climates may be adaptive despite

the low digestibility of mosses generally. This interesting hypothesis deserves further experimental investigation, and arthropod as well as vertebrate herbivores should be considered.

6.6 DIRECTIONS FOR FUTURE RESEARCH

It is evident that we know very little about the nutritional ecology of lichen/moss arthropods. The literature is primarily descriptive, with few attempts to understand the nature of the interactions from either the plant's or the animal's perspective. Future research can therefore go in practically any direction and yield valuable results. In particular, more information on the nutritional requirements of lichen/moss herbivores is needed to understand the various feeding behaviors observed in the field. This information must come from careful laboratory culturing of the herbivores. In addition, we need detailed analyses of the nutritional and secondary chemical composition of lichens and mosses in relation to herbivore feeding. As our understanding of the animals and the plants increases, we will be able to answer questions pertinent to any complete discussion of arthropod nutritional ecology, such as the following:

1. How are herbivore growth and reproductive rates influenced by various lichen/moss foods?
2. In what ways do lichen/moss arthropods alter their performance in response to changes in foods or the environment?
3. To what extent do lichen/moss feeding patterns of herbivores result from differences in food composition, from interspecific competition among the herbivores, or from other factors?
4. Is lichen/moss feeding of greater nutritional benefit to herbivores in harsh physical environments?

These are questions that require knowledge of numerous relatively obscure groups of both plants and animals. It is hoped that those few investigators capable of dealing with these questions will be interested enough in the problems posed in this chapter to begin answering them. For a number of reasons, including the lack of economic importance of the plants, it is likely that research on the nutritional ecology of lichen/moss herbivores will always lag behind that done on higher-plant herbivores. One benefit of this situation is that many concepts and techniques developed by other workers can be put to immediate use by investigators of lichen/moss herbivores. As information accumulates, however, it is becoming apparent that lichen/moss–arthropod interactions are unique in many ways, and this uniqueness demands a level of investigator creativity at least equal to that of higher-plant–arthropod workers.

REFERENCES

- Aleksandrova, V. D., V. N. Andreev, T. V. Vakhtina, R. A. Dydina, G. I. Karev, V. V. Petrovsky, and V. F. Shamurin. 1964. Forage characteristics of the plants in the far north of the USSR. In B. A. Tikhomirov, ed. *The Vegetation of the Far North of the USSR, and Its Utilisation*, Vol. 5. Moskva, Leningrad, pp. 1–484.
- Alexander, C. P. 1920. The crane flies of New York. Part II. Biology and phylogeny. *Cornell Univ. Agr. Exp. Sta. Mem.* **38**, 691–1133.
- Andre, H. 1975. Observations sur les Acariens corticoles de Belgique. *Notes Rech. Fondation Univ. Luxembourgeoise* **4**, 1–31.
- Andre, H. 1979. Notes on the ecology of corticolous epiphyte dwellers. 1. The mite fauna of fruticose lichens. *Rev. Adv. Acarol.* **1**, 551–557.
- Bailey, N. S. 1951. The Tigoidea of New England and their biology. *Entomol. Am.* **31**, 1–140.
- Banerjee, R. D. and S. P. Sen. 1979. Antibiotic activity of bryophytes. *Bryologist* **82**, 141–153.
- Benedetti, R. 1973. Notes on the biology of *Neomachilis halophila* on a California sandy beach (Thysanura: Machilidae). *Pan-Pacif. Entomol.* **49**, 246–249.
- Bergerud, A. T. 1972. Food habits of Newfoundland caribou. *J. Wildlife Manag.* **36**, 913–923.
- Bliss, L. C. 1962. Caloric and lipid content in alpine tundra plants. *Ecology* **43**, 753–757.
- Börner, C. 1952. Die Blattläuse Mitteleuropas, Namen, Synonymie, Wirtspflanzen, Generationszyklen. *Thuringische Bot. Gesell.* **3**, 1–488.
- Brindle, A. 1964. Taxonomic notes on the larvae of British Diptera. No. 18—The Hemerodrominae (Empididae). *Entomologist* **97**, 162–165.
- Broadhead, E. 1958. The psocid fauna of larch trees in northern England. An ecological study of mixed species populations exploiting a common resource. *J. Anim. Ecol.* **27**, 217–263.
- Broadhead, E. and I. W. B. Thornton. 1955. *Elipsocus mclachlani* feeding on lichens. *Oikos* **6**, 1–50.
- Chapman, T. A. 1894. Some notes on *Micro-lepidoptera* whose larvae are external feeders, and chiefly on the early stages of *Erioccephala calthella* (Zygaenidae, Lymacodidae, Erioccephalidae). *Trans. Entomol. Soc. Lond.* **1894**, 335–350.
- Coker, P. D. 1967. Damage to lichens by gastropods. *Lichenologist* **3**, 428–429.
- Coleman, M. J. and H. B. N. Hynes. 1970. The life histories of some Plecoptera and Ephemeroptera in a southern Ontario stream. *Can. J. Zool.* **48**, 1333–1339.
- Colloff, M. J. 1983. Oribatid mites associated with marine and maritime lichens on the island of Great Cumbrae. *Glasg. Nat.* **20**, 347–359.
- Colman, J. 1939. On the faunas inhabiting intertidal seaweeds. *J. Mar. Biol. Assoc. U.K.* **24**, 129–183.
- Courtright, A. M. 1959. Range management and the genus *Rangifer*: A review of selected literature. M.S. thesis, University of Alaska, Fairbanks.
- Erickson, M. and G. E. Miksche. 1974. On the occurrence of lignin or polyphenols in some mosses and liverworts. *Phytochemistry* **13**, 2295–2299.

- Evans, G. O., J. G. Sheals, and D. Macfarlane. 1961. *The Terrestrial Acari of the British Isles*, Vol. 1. British Museum (Natural History), London.
- Fain, A. 1975. Acariens récoltés par le Dr. J. Travé aux Iles Subantartiques. I. Familles Saproglyphidae et Hyadesidae. *Acarologia* **16**, 684–708.
- Fletcher, A. 1973. The ecology of marine (littoral) lichens on some rocky shores of Anglesey. *Lichenologist* **5**, 368–400.
- Forman, R. T. T. 1968. Caloric values of bryophytes. *Bryologist* **71**, 344–347.
- Gerson, U. 1968. Five tydeid mites from Israel (Acarina: Prostigmata). *Isr. J. Zool.* **17**, 191–198.
- Gerson, U. 1969. Moss–arthropod associations. *Bryologist* **72**, 495–500.
- Gerson, U. 1972. Mites of the genus *Ledermuelleria* (Prostigmata: Stigmaeidae) associated with mosses in Canada. *Acarologia* **13**, 319–343.
- Gerson, U. and M. R. D. Seaward. 1977. Lichen–invertebrate associations. In M. R. D. Seaward, ed. *Lichen Ecology*. Academic, London, pp. 69–119.
- Gjelstrup, P. and U. Söchting. 1979. Cryptostigmatid mites (Acarina) associated with *Ramalina siliquosa* (Lichenes) on Bornholm in the Baltic. *Pedobiologia* **19**, 237–245.
- Goering, H. K. and P. J. van Soest. 1970. Forage fiber analyses (apparatus, reagents, procedures and some applications). *USDA Agr. Handb.* **379**, 1–20.
- Grandjean, F. 1936. Les Oribates de Jean Frederick Hermann et de son père. *Ann. Soc. Entomol. Fr.* **105**, 27–110.
- Grandjean, F. 1950. Observations éthologiques sur *Camisia segnis* (Herm.) et *Platynothris peltifer* (Koch) (Acariens). *Bull. Mus. Hist. Nat. Paris* **22**, 224–231.
- Gressitt, J. L. and J. Shoup. 1967. Ecological notes on free-living mites in North Victoria Land. In J. L. Gressitt, ed. *Entomology of Antarctica*. American Geophysical Union, Washington, pp. 307–320.
- Gupta, K. G., and B. Singh. 1971. Occurrence of antibacterial activity in moss extracts. *Res. Bull. Punjab Univ. Sci.* **22**, 237–239.
- Hale, M. E. Jr. 1972. Natural history of Plummers Island, Maryland. XXI. Infestation of the lichen *Parmelia baltimorensis* Gyel. & For. by *Hypogastrura packardi* Folsom (Collembola). *Proc. Biol. Soc. Washington* **85**, 287–296.
- Harding, D. J. L. and R. A. Stuttard. 1974. Microarthropods. In C. H. Dickinson and G. J. F. Pugh, eds. *Biology of Plant Litter Decomposition*, Vol. 2. Academic, London, pp. 489–532.
- Holden, M. and M. V. Tracey. 1950. A survey of enzymes that can break down tobacco-leaf components. 2. Digestive juice of *Helix* on defined substances. *Biochem. J.* **47**, 407–414.
- Holloway, B. A. 1970. A new genus of New Zealand Anthribidae associated with lichens (Insecta: Coleoptera). *N.Z. J. Sci.* **13**, 435–446.
- Hughes, A. M. and P. J. Tillbrook. 1966. A new species of *Calvolia* (Acaridae, Acarina) from the South Sandwich Islands. *Bull. Br. Antarct. Surv.* **10**, 45–53.
- Iskandar, I. K. and J. K. Syers. 1971. Solubility of lichen compounds in water: Pedogenetic implications. *Lichenologist* **5**, 45–50.
- James, P. W. and A. Henssen. 1976. The morphological and taxonomic significance of cephalodia. In D. H. Brown, D. L. Hawksworth, and R. H. Bailey, eds. *Lichenology: Progress and Problems*. Academic, London, pp. 27–77.

- Janetschek, H. 1967. Arthropod ecology of South Victoria Land. In J. L. Gressitt, ed. *Entomology of Antarctica*. American Geophysical Union, Washington, pp. 205–293.
- Jones, J. R. E. 1949. A further ecological study of calcareous streams in the “Black Mountain” district of South Wales. *J. Anim. Ecol.* **18**, 142–159.
- Kalshoven, L. G. E. 1958. Observations on the black termites, *Hospitalitermes* sp., of Java and Sumatra. *Insectes Soc.* **5**, 9–30.
- Kühnelt, W. 1976. *Soil Biology, with Special Reference to the Animal Kingdom*, 2d Ed. Faber, London.
- Laundon, J. R. 1971. Lichen communities destroyed by psocids. *Lichenologist* **5**, 177.
- Lawrey, J. D. 1977. Litter decomposition and trace metal cycling studies in habitats variously influenced by coal strip-mining. Ph.D. dissertation, Ohio State University, Columbus.
- Lawrey, J. D. 1980. Correlations between lichen secondary chemistry and grazing activity by *Pallifera varia*. *Bryologist* **83**, 328–334.
- Lawrey, J. D. 1983. Lichen herbivore preference: A test of two hypotheses. *Am. J. Bot.* **70**, 1188–1194.
- Lawrey, J. D. 1984. *Biology of Lichenized Fungi*. Praeger, New York.
- Maass, W. S. C. and J. S. Craigie. 1964. Examination of some soluble constituents of *Sphagnum* gametophytes. *Can. J. Bot.* **4**, 805–813.
- Madsen, G. C. and A. L. Pates. 1952. Occurrence of antimicrobial substances in chlorophyllose plants growing in Florida. *Bot. Gaz.* **113**, 293–300.
- Mani, M. S. 1964. *Ecology of Plant Galls*. W. Junk, The Hague.
- McCleary, J. A. and D. L. Walkington. 1966. Mosses and antibiosis. *Rev. Bryol. Lichenol.* **34**, 309–314.
- McCleary, J. A., P. S. Sypherd, and D. L. Walkington. 1960. Mosses as possible source of antibiotics. *Science* **131**, 108.
- McDonogh, R. S. 1939. The habitat, distribution and dispersal of the psycid moth, *Luffia ferchaultella*, in England and Wales. *J. Anim. Ecol.* **8**, 10–28.
- McMillan, J. H. and I. N. Healey. 1971. A quantitative technique for the analysis of the gut contents of Collembola. *Rev. Ecol. Biol. Sol.* **8**, 295–300.
- Michael, A. D. 1883–1887. *British Oribatidae*. Ray Society, London.
- Miksche, G. E. and S. Yasuda. 1978. Lignin of “giant” mosses and some related species. *Phytochemistry* **17**, 503–504.
- Nielsen, C. O. 1963. Laminarinases in soil and litter invertebrates. *Nature* **199**, 1001.
- Pakarinen, P. and D. H. Vitt. 1974. The major organic components and caloric contents of high arctic bryophytes. *Can. J. Bot.* **52**, 1151–1161.
- Pates, A. L. and G. C. Madsen. 1955. Occurrence of antimicrobial substances in chlorophyllose plants growing in Florida. II. *Bot. Gaz.* **116**, 250–261.
- Peake, J. F. and P. W. James. 1967. Lichens and Mollusca. *Lichenologist* **3**, 425–428.
- Plitt, C. C. 1907. *Webera sessilis* and ants. *Bryologist* **10**, 54–55.
- Plitt, C. C. 1934. A lichen-eating snail. *Bryologist* **37**, 102–104.

- Prins, H. H. T. 1981. Why are mosses eaten in cold environments only? *Oikos* **38**, 374–380.
- Pryor, M. E. 1962. Some environmental features of Hallett Station, Antarctica, with special reference to soil arthropods. *Pacif. Insects* **4**, 681–728.
- Ramaut, J. L. 1959. Autoecologie du genre *Sphagnum*. *Nat. Belges* **40**, 9–22.
- Rastorfer, J. R. 1976. Caloric values of three Alaskan–Arctic mosses. *Bryologist* **79**, 76–78.
- Richardson, D. H. S. 1975. *The Vanishing Lichens*. David & Charles, Vancouver, Canada.
- Richardson, D. H. S. and C. M. Young. 1977. Lichens and vertebrates. In M. R. D. Seaward, ed. *Lichen Ecology*. Academic, London, pp. 121–144.
- Ross, E. S. 1966. A new species of Embioptera from the Galápagos Islands. *Proc. Calif. Acad. Sci.* **34**, 499–504.
- Rundel, P. W. 1978. The ecological role of secondary lichen substances. *Biochem. Syst. Ecol.* **6**, 157–170.
- Runham, N. W. 1975. Alimentary canal. In V. Fretter and J. Peake, eds. *Pulmonates*, Vol. I: *Functional Anatomy and Physiology*. Academic, London, pp. 53–104.
- Runham, N. W. and P. J. Hunter. 1970. *Terrestrial Slugs*. Hutchinson University Library, London.
- Schuster, R. 1956. Der Anteil der Oribatiden an den Zersetzungs Vorgängen in Boden. *Z. Morph. Oekol. Tiere* **45**, 1–33.
- Seaward, M. R. D. 1965. Lincolnshire psocids. *Trans. Lincolnshire Nat. Union* **16**, 99–100.
- Seaward, M. R. D. 1975. Contributions to the lichen flora of southeast Ireland. I. *Proc. R. Ir. Acad.* **75B**, 185–205.
- Sengbusch, H. G. 1954. Studies on the life history of three oribatid mites, with observations on other species. *Ann. Entomol. Soc. Am.* **47**, 646–667.
- Seyd, E. L. and M. R. D. Seaward. 1984. The association of oribatid mites with lichens. *Zool. J. Linn. Soc.* **80**, 369–420.
- Sigal, L. L. 1984. Of lichens and lepidopterons. *Bryologist* **87**, 66–68.
- Skre, O., A. Berg, and F. E. Wielgolaski. 1975. Organic compounds in alpine plants. In F. E. Wielgolaski, ed. *Fennoscandian Tundra Ecosystems*, Part 1. *Plants and Microorganisms*. Springer, Berlin, pp. 339–350.
- Slansky, F., Jr. 1979. Effect of the lichen chemicals atranorin and vulpinic acid upon feeding and growth of larvae of the yellow-striped armyworm, *Spodoptera ornithogalli*. *Environ. Entomol.* **8**, 865–868.
- Smith, A. L. 1921. *Lichens*. Cambridge University Press, Cambridge, England.
- Stahl, G. E. 1904. Die Schutzmittel der Flechten gegen Tierfrass. In *Festschrift z. 70. Geburtstage von Ernst Haeckel*. Fischer, Jena, East Germany, pp. 357–375.
- Stebaev, I. V. 1963. Die Veränderung der Tierbevölkerung der Boden im Laufe der Bodenentwicklung auf Felsen und auf Verwitterungsprodukten im Wald-Wiesenlandschaften des Süd-Urals. *Pedobiologia* **2**, 265–309. (in Russian).
- Stephenson, N. L. and P. W. Rundel. 1979. Quantitative variation and the ecological role of vulpinic acid and atranorin in the thallus of *Letharia vulpina* (Lichenes). *Biochem. Syst. Ecol.* **7**, 263–267.

- Strong, J. 1967. Ecology of terrestrial arthropods at Palmer Station, Antarctic Peninsula. In J. L. Gressitt, ed. *Entomology of Antarctica*. American Geophysical Union, Washington, pp. 357-371.
- Tilbrook, P. J. 1967. The terrestrial invertebrate fauna of the maritime Antarctic. *Phil. Trans. R. Soc. B* **252**, 261-278.
- Tillyard, R. J. 1923. On the larva and pupa of the genus *Sabatinca* (order Lepidoptera, family Micropterygidae). *Trans. Entomol. Soc. Lond.* **1922**, 437-453.
- Tillyard, R. J. 1926. *The Insects of Australia and New Zealand*. Angus and Robertson, Sydney.
- Travé, J. 1961. Contribution à l'étude des Oribatulidae (Oribates, Acariens). *Vie Milieu* **12**, 315-351.
- Travé, J. 1963. Ecologie et biologie des Oribates (Acariens) saxicoles et arboricoles. *Vie Milieu (Suppl.)* **14**, 1-267.
- Travé, J. 1969. Sur le peuplement des lichens crustacés des Iles Salvages par les Oribates (Acariens). *Rev. Ecol. Biol. Sol.* **6**, 239-248.
- Vartia, K. O. 1973. Antibiotics in lichens. In V. Ahmadjian and M. E. Hale Jr., eds. *The Lichens*. Academic, New York, pp. 547-561.
- Verdcourt, B. 1947. A note on the food of *Acrydium* Geoff. (Orthopt.). *Entomol. Monthly Mag.* **83**, 190.
- Wessels, D. C., L. A. Wessels, and W. H. Holzapfel. 1979. Preliminary report on lichen-feeding Coleoptera occurring on *Teloschistes capensis* in the Namib Desert, South West Africa. *Bryologist* **82**, 270-273.
- Wieser, W. 1963. Adaptations of two intertidal isopods. II. Comparison between *Campeopea hirsuta* and *Naesa bidentata* (Sphaeromatidae). *J. Mar. Biol. Assoc. U.K.* **43**, 97-112.
- Wolters, B. 1964. Die Verbreitung antifungaler Eigenschaft bei Moosen. *Planta* **62**, 88-96.
- Woodring, J. P. 1963. The nutrition and biology of saprophytic Sarcopitiformes. *Adv. Acarol.* **1**, 89-111.
- Woodring, J. P. and E. F. Cook. 1962. The biology of *Ceratozetes cisalpinus*, *Scheloribates laevigatus*, and *Oppia neerlandica* (Oribatei), with a description of all stages. *Acarologia* **4**, 101-137.
- Yom-Tov, Y. and M. Galun. 1971. Note of feeding habits of the desert snails *Sphincterochila boissieri* Charpentier and *Trochoidea (Xerocrassa) seetzeni* Charpentier. *Veliger* **14**, 86-88.
- Young, S. R. and W. Block. 1980. Some factors affecting metabolic rate in an Antarctic mite. *Oikos* **34**, 178-185.
- Zopf, W. 1896. Zur biologischen Bedeutung der Flechtensäuren. *Biol. Centralbl.* **16**, 593-610.
- Zopf, W. 1907. Biologische und morphologische Beobachtungen an Flechten. III. Durch tierische Eingriffe hervorgerufene Gallenbildungen an Vertretern der Gattung *Ramalina*. *Ber. Dsch. Bot. Ges.* **25**, 233-237.
- Zukal, H. 1895. Morphologische und biologische Untersuchungen über die Flechten. *Sber. K. Böhm. Ges. Wiss. Math.-Nat. Kl.* **104**, 1303-1395.